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Forced Dissociation of Food- and Light-Entrainable Circadian Rhythms of Rats in a Skeleton Photoperiod

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BRINKHOF, M. W. G., S. DAAN AND J. H. STRUBBE. *Forced dissociation of food- and light-entrainable circadian rhythms of rats in a skeleton photoperiod.* PHYSIOL BEHAV **65**(2) 225–231, 1998.—To investigate the control over drinking and feeding behavior by the light-entrainable circadian pacemaker, rats were maintained in a 12 h:12 h skeleton photoperiod for 36 days with both food and water restricted to the subjective day. During the restriction period most of the food and water intake was concentrated during the first 4 h of the subjective day. The subsequent release into ad lib conditions under the skeleton photoperiod or continuous dark showed that this increased ingestion during the subjective day persisted for up to 6–10 days. This may indicate the entrainment of a food-entrainable oscillator, which has hitherto been investigated solely in anticipatory activity. The daily activity rhythm returned to its original phase position. Thus the phase of the overt daily rhythm is eventually only determined by the phase of the light-entrainable oscillator (LEO) but can temporarily be influenced by the restriction of food and water access. This restriction apparently stimulated a food-entrainable oscillator in antiphase with the light-entrainable oscillator but failed to phase shift or entrain the light-entrainable oscillator. © 1998 Elsevier Science Inc.

Feeding behavior Drinking behavior Circadian pacemaker Food-entrainable oscillator
Food and water deprivation Body mass

FEEDING and drinking of rats occur mainly during the dark phase of the light–dark cycle. Feeding and drinking activity of Wistar rats fed on a normal laboratory diet shows a bimodal or trimodal distribution over the dark phase with peaks at dawn and dusk (3,9,12). Under ad lib. conditions a close temporal association exists between feeding and drinking so that 70–90% of the daily water intake occurs around meals (1,13). In contrast, when feeding behavior is restricted to the light phase, only a small amount of water intake is food-associated, in spite of no change of total daily water intake (13). This dissociation can partly be attributed to negative masking ("light aversion") of drinking behavior by light. Under a skeleton photoperiod (SPP), with food access only in the dark interval corresponding with the subjective day, drinking during this interval was increased, although half of the water intake occurred during the subjective night (19). Apparently drinking is partly under control of the light-entrained circadian pacemaker located in the suprachiasmatic nucleus (SCN), partly directly stimulated by food intake. Evidence for this was also obtained by others (3,4). Therefore, one might presume that SCN-controlled drinking in the subjective night exerts phase control over feeding behavior, such that feeding is rapidly reallocated to the subjective night after reinstitution of ad lib. conditions.

Although the pattern of feeding behavior is largely controlled by a circadian oscillator in the SCN, there is also evidence for a food-entrainable oscillator (FEO) (10,11,15,20). The FEO is anatomically distinct from the SCN and is expressed in meal anticipatory activity under circadian cycles of meal availability (3,10,15). There is no evidence for the existence of a water entrainable-oscillator, but the combination of restriction of water and food potentiate the appearance of the FEO (10). To discern the influences of FEOs and light-entrainable oscillators (LEOs), we induced in the present study a maximal phase discrepancy between the food-entrainable and light-entrainable components of their circadian systems by maintaining rats under a 12-h skeleton photoperiod (SPP) with both food and water restricted during 36 days to the subjective day. The temporal characteristics of feeding and drinking in rats after release from food and water restriction into ad lib. conditions were then investigated under SPP as well as under continuous dark (DD) conditions. This DD condition was introduced to determine whether food and water restriction caused a phase shift of the LEO system. This showed that under these conditions the food-entrained components remain discernible for up to 10 days, whereas the phase of the nocturnal rhythm in

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ingestive behavior is apparently solely determined by the phase of the light-entrainable pacemaker.

METHODS

Male Wistar rats, about 3 months old and weighing 280–340 g (mean 310 g) at the start of the experiment, were kept in a climate room which was adequately screened from laboratory noise. Entrance into the room was through a light gate. The rats were individually housed in perspex cages. Each cage consisted of an outcage (40 × 40 × 40 cm) with a dark perspex nest box (20 × 20 × 20 cm) attached to the outside of the cage. Entrance into the nest box was through a 4 × 4 cm opening. The nest box contained wood shavings for bedding whereas the outcage had a rigid wire mesh floor. Except during the restriction periods, food pellets (Hopefarms, The Netherlands) in hoppers and water in bottles were available ad lib. The food hopper and water bottle were situated opposite of each other in the outcage at the distant ends from the nest box. Food hoppers and water bottles were filled regularly, about two times per week. The access to food and water was controlled by means of horizontally sliding doors. Lighting in the room was provided by three overhead 40-W daylight type fluorescent tubes. Light intensity, measured with a UDT Model 40 optometer using a radiometric filter and a candle diffuser, was the same for all rats and varied between 4 $\mu W/cm^2$ at cage floor level to about 20 $\mu W/cm^2$ at the level of the food hopper. Light intensity inside the nest box was very low (1 $\mu W/cm^2$). Room temperature was thermostatically controlled at 21°C. Relative humidity was constant at 60%.

Recording

Feeding and drinking activity and the occupation of the outcage and nest box were recorded continuously throughout the experiment on a 20-channel Esterline-Angus event recorder. The gnawing and biting of food pellets from the food hoppers through stainless steel bars caused the hopper to swing slightly. The electrical signal caused by this movement resulted in a pen deflection on the event recorder. Spillage was collected in an undertray attached to the hopper. The daily amount of spillage ranged from 0.05 to 0.2 g. Drinking activity was recorded by means of an L-shaped stainless steel pedal, situated below the water bottle with a horizontal lip just in front of the drinking spout. Outcage occupation was recorded by means of a wire mesh tilt floor, which was pivoted along the middle. Microswitches were situated at each corner of the outcage beneath the floor. When the rat was in the outcage the floor was tilted and one or two microswitches were depressed. This produced a deflection on the recording paper. Absence of a deflection indicated that the rat was in its nest.

Experimental Procedures

Habituation/baseline. Seven rats from our colony were given a 3-week habituation period with food and water available ad lib. on a normal light–dark cycle (LD 12:12). Next a SPP (LD 0.67:11.33) was introduced (Days 1–12), with two 40-min light pulses presented per day, each centered on the clock time when light transitions occurred during the preceding LD 12:12 condition (i.e., every 12 h at the start of the subjective day and the subjective night (for definitions, see (5)). Food and water were still freely available.

Experimental period. Following this baseline period, food and water were restricted to the subjective day for 36 days (Days 13–48). Thereafter, food and water were freely available again for 26 days. During the postexperimental period the rats were divided into two groups kept under different photoperiod regimes. Group 1 ($n = 3$) stayed under the SPP conditions for the next 18 days (Days 49–66) and, thereafter, under the original LD 12:12 conditions for 8 days (Days 67–74). Group 2 ($n = 4$) was placed in DD for the whole 26 days postexperimental period (Days 49–74) for reasons explained in the Results.

Food Intake, Water Intake, and Body Weight

Food intake, water intake, and body weight were measured once a day on most occasions when the lights were on. For practical reasons, overall daily food intake, water intake, and body weight were not obtained under DD in Group 2.

RESULTS

Habituation and Baseline Period

Figures 1 and 2 show continuous records of the outcage occupation and of the feeding and drinking activity. As is typical for the nocturnal rat under LD, feeding and drinking are mainly confined to the dark segment of the LD cycle. When feeding occurs during the light phase, all rats showed so-called "procuring behavior" during feeding (19). Instead of eating and gnawing pieces of food in the vicinity of the food hopper as was usual during the dark phase, a rat quickly returned with each bite to the nest box and ate it there. After 6 days the rhythm is relatively stable.

With the introduction of SPP with food and water continuously available, all rats showed a slight increase in feeding and drinking activity during the last 2–3 h of the subjective day. Drinking activity occurred in close temporal association with feeding, and the timing of meals and drinks was fairly constant over the successive days. Occupation of the outcage during the subjective day was mostly associated with feeding and drinking activity. Procuring behavior (see above) was absent during the subjective day. Throughout the SPP baseline, period feeding and drinking activity remained predominantly distributed over the subjective night, with a principal concentration in the beginning (dusk peak; 1300–1500 hours) and another toward the end (dawn peak; 2130–2330 hours). In some rats a third concentration was evident in the middle (1630–1930 hours) of the subjective night.

Food and Water Restriction (FWR) Period

On the first day when food and water were restricted to the subjective day (Days 13–48; Figs. 1 and 2), the rats first entered the outcage after approximately 1–4 h. Over the next 3–4 days the start of activity was gradually advanced until the rats immediately entered the outcage to eat and drink. From Day 20 on, the temporal distribution of feeding and drinking activity and outcage occupation on the subjective day were reasonably stable in the individual animals. Different rats showed a clear resemblance in these activity patterns. The most striking aspect was that the vast part of the daily feeding and drinking activity was concentrated in the first 5 h of the subjective day. In this first half of the subjective day, two periods could be discriminated. First, immediately after the start of the subjective day all rats entered the outcage and showed feeding activity. Subsequently, the first drinks occurred, sometimes alternated with meals. This activity period lasted 30–60 min, during which the outcage was almost continuously occupied, and was followed by a period during which no feeding and drinking activity occurred. The rats returned to their nest boxes for approximately 1 h (rats 1, 2, 3, 6, and 7). Second, most rats showed a large concentration of feeding and drinking in the next 3–5 h of the first half of the subjective day (subjective day peak). Two rats (rats 4 and 5) showed an extreme compression of feeding

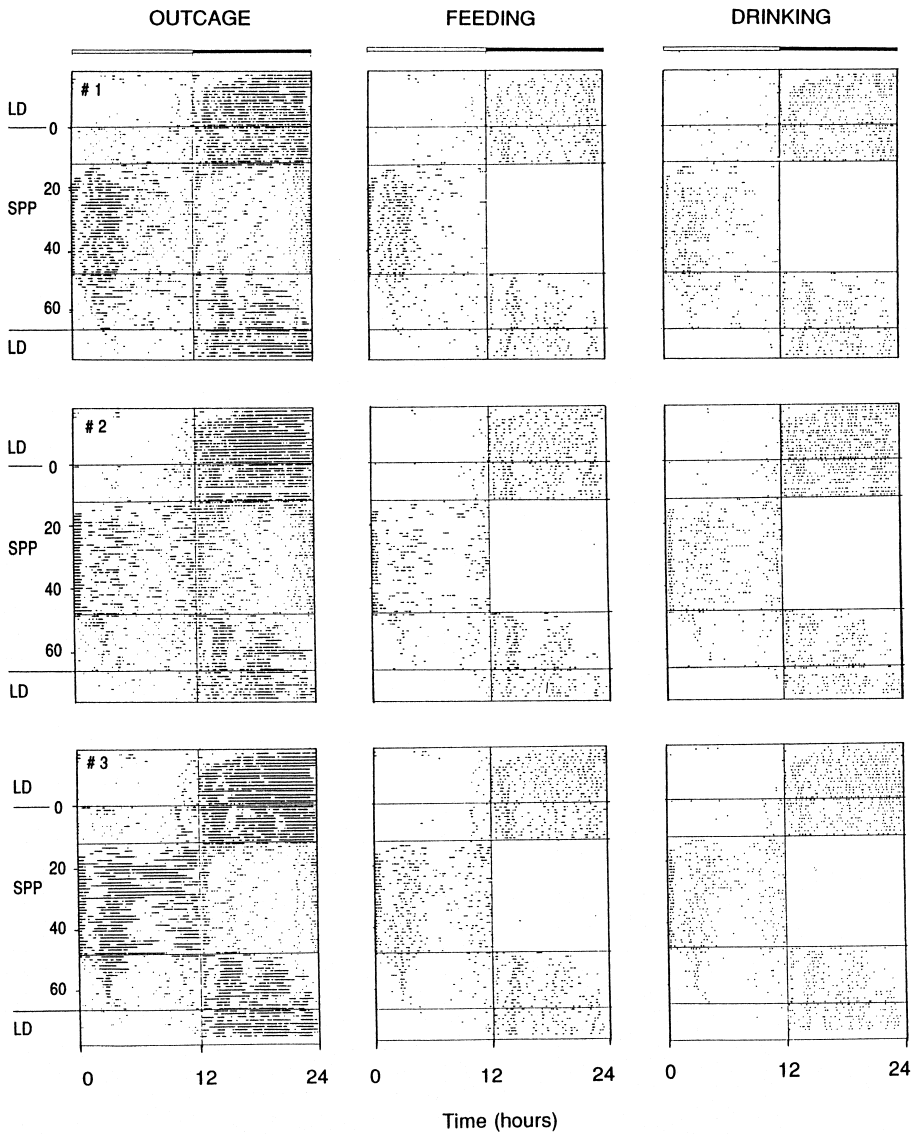

FIG. 1. Distribution of feeding, drinking, and outcage occupation over the daily cycle by three rats (rats 1–3). The lighting conditions were changed from light–dark (LD) 12:12 to a skeleton photoperiod (SPP) on Day 0. The white and black bars at the top indicate the subjective day and night phase under SPP. Notice the rapid return of activity in the beginning ("dusk") and in the middle of the subjective night upon reinstating the ad lib. condition. No activity was initially seen at the end of the subjective night ("dawn"), whereas a gradually dampening peak in activity was seen in the first half of the subjective day.

and drinking activity in the first half of the subjective day. Toward the end of the FWR period (from Day 30 onward), almost the complete daily food and water intake was achieved in only 3–4 h (clock time $\approx$ 0100–0400 hours). Thereafter, these rats stayed in the nest box for most of the subjective day. In the other rats, where the subjective day peak was less concentrated, further feeding and drinking activity was observed toward the end of the subjective day (Days 13–48).

In the subjective night of the FWR period (Days 13–48), all rats strongly reduced the total duration of outcage occupation from the first day onward. Visits to the outcage were short and concentrated in the dusk, middle, and dawn period, i.e., the customary times of activity during the preceding baseline condition (Days 1–12).

Return to Ad Lib. under SPP (Group 1)

Among the rats maintained under SPP conditions (Group 1), the vast part of both the daily feeding and drinking activity immediately returned to the subjective night once the ad lib. food and water availability was restored (Fig. 1) (Days 49–66). However, whereas feeding and drinking were observed during the dusk and the middle period from the first day onward, the rats almost completely refrained from ingestive behavior during the dawn period for nearly 2 weeks and stayed in their nest box for most of the time (Days 49–62). At the same time, there was considerably more feeding and drinking activity during the subjective day (Days 49–66) than under the initial baseline condition (Days 1–12). In particular, the striking peak in general activity, which emerged

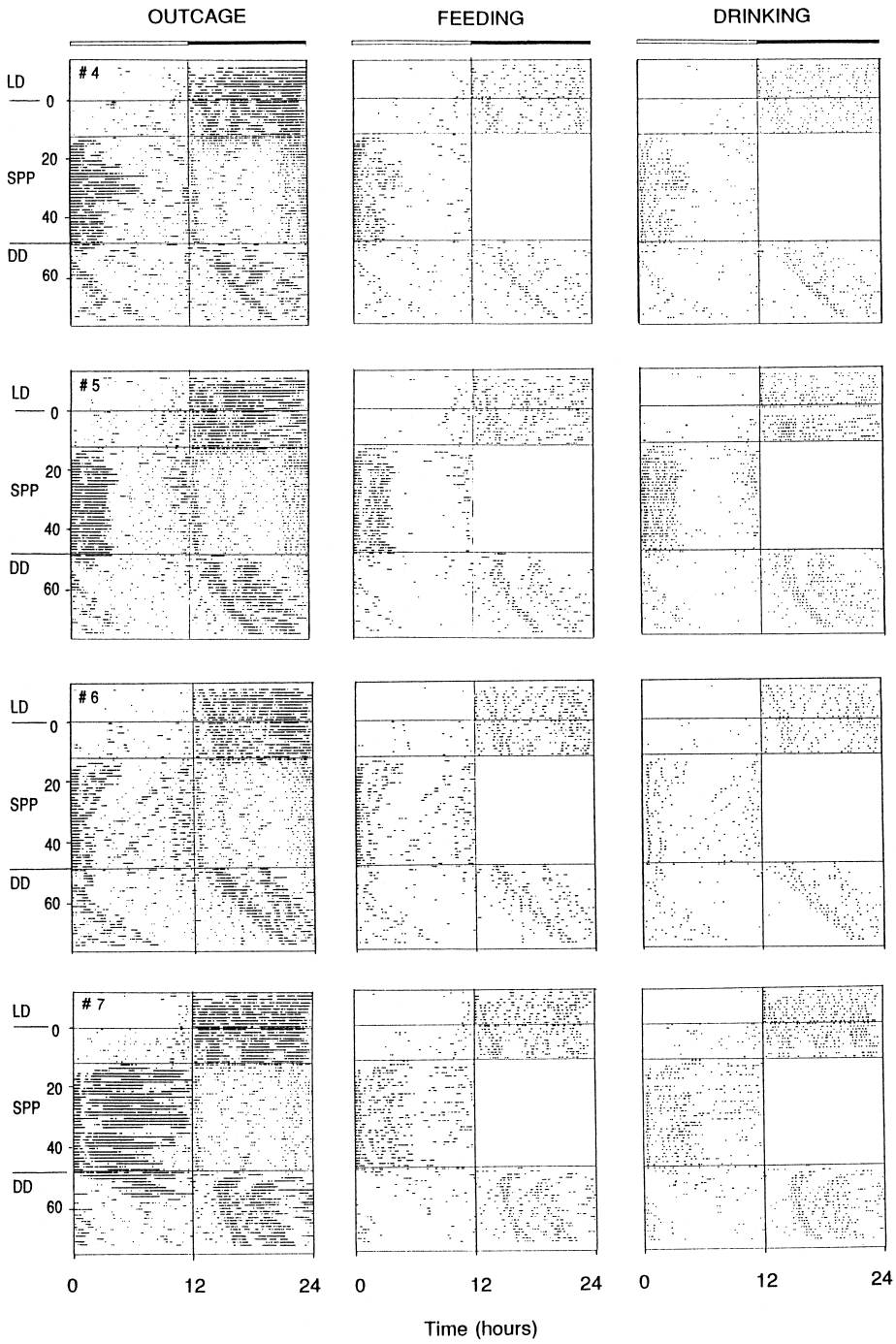

FIG. 2. Distribution of feeding, drinking, and outcage occupation over the daily cycle by four rats (rats 4–7). The lighting conditions were changed from light–dark (LD) 12:12 to a skeleton photoperiod (SPP) on Day 0. The white and black bars at the top indicate the light and dark phases or subjective phases under SPP. Notice the absence of transients in activity between the fading of the peak in the first half of the subjective day and the reappearance of the predawn peak.

under the FWR conditions (subjective day peak), persisted for at least 2 weeks. During this period the subjective day peak gradually dampened and, when about faded, feeding and drinking behavior reappeared at dawn, thereby reestablishing the original activity pattern during the subjective night phase. The final return to the initial light–dark schedule (Days 67–74) completely restored the original, nocturnal activity rhythm (Days −21 to 0).

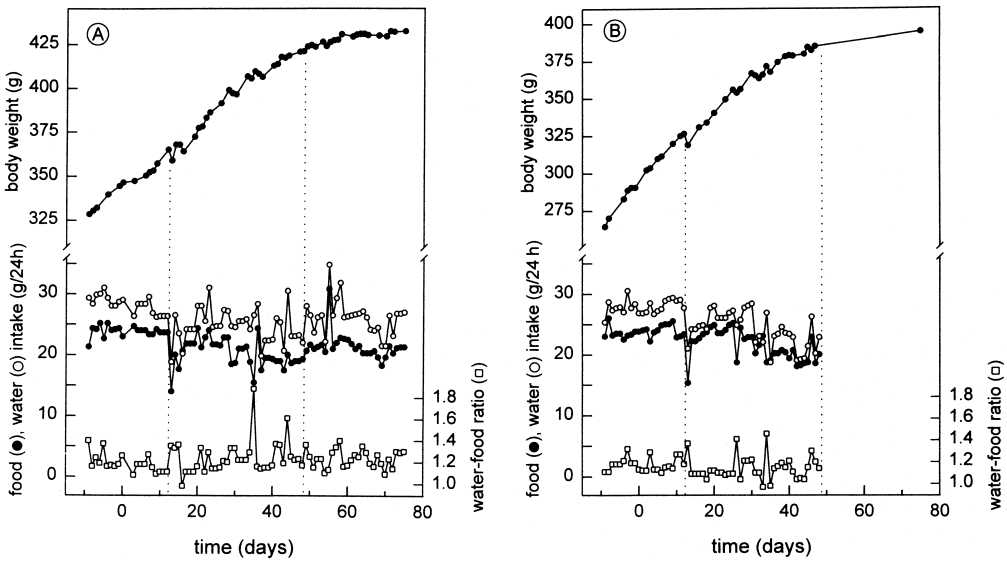

FIG. 3. Effects of food and water restriction to the subjective day (Days 13–48) on body weight, on water and food intake, and on the mean ratio of water and food intake in Group 1 (A) and Group 2 (B). The lighting conditions were changed from light–dark (LD) 12:12 to a skeleton photoperiod (SPP) on Day 0.

Return to Ad Lib. under DD (Group 2)

To investigate whether the subjective day peak was actually caused by a phase shift of a dawn oscillator under the FWR conditions, we kept Group 2 under constant dark once the ad lib. food and water availability was restored (Fig. 2; Days 49–74). Under the SPP conditions of Group 1 feeding and drinking behavior might have been suppressed during the lights-on stage at dawn (clock time ≈ 2340–0020 hours), thereby masking behavioral transients in the 2 weeks between the dampening of the subjective day peak and the return of the dawn peak (Group 1; Fig. 1, Days 49–66).

In the absence of the synchronizing effect of the SPP, a free-running circadian rhythm was now observed with activity in the subjective night with a period (τ) of approximately 24.5 h, as typical for rats. Similar to Group 1, all rats in Group 2 instantly relocated the vast part of the daily feeding and drinking activity to their subjective night on return to ad lib. food and water availability (Fig. 2, Days 49–74). Furthermore, the rats in Group 2 refrained from feeding and drinking during the dawn period in the first few days, and a dampening subjective day peak was observed as well. Yet the dampening of the subjective day peak and the return of activity during the dawn period occurred much faster under DD (Group 2) than under SPP conditions (Group 1). In three rats kept under DD (rats 4-6) the subjective day peak lasted for 5–6 days, whereas under SPP conditions (Group 1) this activity peak persisted for at least 2 weeks. Only rat 7 showed a subjective day peak of similar duration, i.e., 12 days (Days 49–60). At dawn, feeding and drinking activity reappeared after 5–6 days under DD conditions (Group 2). In particular, transients in feeding and drinking activity between the disappearance of the subjective day peak and the reappearance of the dawn peak were absent in most rats of Group 2 (rats 4, 5, and 7; Fig. 2, Days 49–55).

Food Intake, Water Intake, and Body Weight

In analyzing the total daily food and water intakes, we used multiple regression and controlled for individual differences in the level of consumption. The mean daily food and water intakes were not significantly different between the baseline LD and the SPP conditions in Groups 1 and 2 (Fig. 3): food intake, $F(1, 140) = 1.29$, $p = 0.26$; water intake, $F(1, 140) = 0.31$, $p = 0.58$. Furthermore, confined to the baseline SPP condition (Days 1–12), both food intake and water intake were stable over successive days in individual rats (for time trend in food intake, $F(1, 70) = 2.53$, $p = 0.12$; water intake, $F(1, 70) = 0.70$, $p = 0.41$). Among the three experimental periods under SPP conditions (i.e., pre-experimental baseline ad lib., FWR, and postexperimental ad lib.), both food intake and water intake differed significantly [$F(2, 375) = 38.75$, $p < 0.001$ and $F(2, 375) = 6.55$, $p = 0.002$, respectively]. During the FWR period (Days 13–48) all rats showed a similar decrease (mean −0.13 g/day) in the daily food intake (Fig. 3); for the time trend: $F(1, 237) = 50.01$, $p < 0.001$). Rat 7 used an excessive amount of water, i.e., 45.5 (SE 2.5) g/day compared to 24.5 (SE 0.5) g/day in the remaining six individuals, and was, therefore, excluded from further analyses. Among the remaining six rats (rats 1–6) water intake decreased significantly during the FWR period as well [Fig. 3; $F(1, 203) = 16.60$, $p < 0.001$]. Overall, both the daily intake of food [$F(1, 269) = 52.14$, $p < 0.001$] and the daily intake of water [$F(1, 269) = 39.70$, $p < 0.001$] were significantly reduced during the FWR period compared to the preceding baseline period. On return to ad lib. under SPP conditions (Group 1 only), both the daily food intake [$F(1, 190) = 15.39$, $p < 0.001$] and the daily water intake [$F(1, 190) = 11.53$, $p < 0.001$] were elevated compared to the FWR period, but whereas water use returned to pre-experimental baseline levels [$F(1, 80) = 0.21$, $p = 0.21$], food consumption remained significantly lower [$F(1, 80) = 15.36$, $p < 0.001$]. The water to food ratio did not vary significantly between the pre-experimental ad lib., the FWR, and the postexperimental ad lib. SPP conditions [$F(2, 328) = 0.85$, $p = 0.43$; Fig. 3]. Finally, despite the significant decrease in food consumption during the experimental period, all rats increased in body mass as normal (Fig. 3).

DISCUSSION

The present results showed that long-term restriction of food and water availability to the subjective day period of a SPP condition does

not lead to permanent fixation of the behavior at that time. Upon reinstitution of the ad lib. condition, most feeding and drinking activity instantly returned to its original position in the dusk and middle period of the subjective dark phase. However, the rats refrained from feeding and drinking prior to subjective dawn for about 2 weeks, whereas a novel, now dampening peak in these behaviors was seen in the first half of the subjective day phase (Group 1). This subjective day peak, which came to expression under the restriction conditions, was apparently not caused by a phase-shifted dawn oscillator. Under constant dark conditions no transients in feeding and drinking activity were seen between the fading subjective day peak and the reappearance of the predawn peak (Group 2). This suggested that the output of the circadian oscillator originally generating the predawn peak was temporarily reduced or obstructed.

It is remarkable that virtually no feeding and drinking behavior was observed prior to dawn upon the return to ad lib. conditions for about 14 days under SPP conditions (Group 1) and for about 5 days under DD conditions (Group 2). When experimentally restricting either food for 10 days (19), or water for 36 days (unpublished data) to the subjective day, the predawn peak in activity instantly returned. In previous studies (14,18) in which the interaction between the circadian and the caloric control of food intake was investigated, it was concluded that the motivation to feed prior to dawn is under control of a circadian LEO. The high motivation to feed prior to dawn persisted when the access to food was blocked during that period for 3 weeks (14). Furthermore, intragastric infusion of liquid food effectively suppressed food intake during the first half, but not during the second half, of the dark phase, indicating that signals from calories are largely neglected or overruled at dawn (18). This makes it unlikely that enhanced food intake in the first half of the subjective day upon the return to ad lib. conditions (i.e., the persisting subjective day peak) suppressed the motivation to feed prior to dawn through energy regulation. More likely, the output of the underlying pacemaker was temporarily reduced or its behavioral expression obstructed by some other mechanism, related to the simultaneous expression of the subjective day peak. The immediate return of the predawn peak following the restriction of food (19) to the subjective day is in accordance with this view, as the subjective day peak in feeding and drinking activity did not evolve under such experimental conditions.

What could be the cause for the persisting subjective day peak after the return to ad lib. conditions? The situation during the restriction period, where rats concentrated the bulk of their daily food and water intake in just 4–5 h, has similarities to experiments using daily schedules with just a few hours of food or water access. Such schedules of periodic food availability have demonstrated the existence of a separate FEO (3,6,10,11,15–17). The primary manifestation of the FEO is in anticipatory activity prior to daily food access (2,3), but it is also expressed in plasma corticosterone (7). The concentration of feeding in the early subjective day phase under the present experimental conditions is similar to the situation in imposed feeding schedules and may have provided the conditions for the entrainment of the FEO. Therefore, sustained activity of the FEO after the return to ad lib. conditions may explain the persistence of the subjective day peak.

The involvement of the FEO would also explain the parallel occurrence of the subjective day peak and the behavioral quiescence at dawn in ad lib, if the FEO is in some way coupled to the LEO system located in the SCN. Previous studies using restricted feeding under LL or DD have shown that rats display strong anticipation of feeding time without entrainment of their free-running circadian rhythms (3,6,16). However, changes in the period or the phase of the light-entrainable rhythm during or after a period of restricted feeding (6,15,16) do suggest a weak coupling between the two pacemaker systems. In rabbits (8) and hamsters (10,11) the coupling between FEO and LEO appears much stronger, as free-running rhythms usually entrained to feeding time. After the termination of feeding schedules, feeding-entrained activity rhythms generally vanish quickly. This contrasts with the results of the present study, where feeding activity in the subjective day remained discernible for at least 10 days under SPP. Moreover, during this period ingestive behavior was almost absent at dawn.

After termination of the food restriction schedule, the FEO-determined activity in the subjective day disappears more rapidly when free running in DD than when the system is left entrained by the skeleton photoperiod. An explanation is hard to give, but it is possible that the FEO runs at a different frequency from the LEO, whereby its separate expression disappears when they get into phase with each other.

Aschoff (2) suggested that a distinct FEO system may allow the rat to adjust physiological and behavioral responses involved in the location, consumption, and digestion of food to specific times of day without phase-shifting the main circadian pacemaker system. In this sense, three effects, possibly related to the FEO, are noteworthy in the present study. First, by concentrating the bulk of the daily food and water intake in only 4–5 h during the FWR period, the rats reduced the activity time during the subjective day where under natural conditions the risk of predation might be highest. Second, although food intake was significantly reduced during the FWR period, the concomitant overall reduction in the total activity time over the day–night cycle may have reduced the daily energy expenditure and permitted normal gain in body weight (Fig. 3). Third, by concentrating the bulk of the daily food and water intake in just a few hours, the rats were able to accomplish a major part of the daily sleep in the preferred day time.

The return to the ad lib. condition clearly showed that the rat's motivation to concentrate most of the food and water intake in the original subjective dark period had persisted during the FWR period. This was also indicated by the persistence of the bi- or trimodal pattern in the outcage occupation in the subjective dark period during the restriction period. This implies that the combined, long-term restriction of food and water access to the subjective day period had failed to entrain the major circadian pacemaker system in the SCN. Furthermore, the initially persisting subjective day peak failed to influence the phase of the light-entrainable pacemaker after the entraining light signals were discontinued.

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